A review of the methods for studying biotic interactions in phenological analyses

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Abstract:

1. Phenological events play a key role modulating ecosystem services; however, the complex and interlinked nature of ecosystems means interactions among different taxa during phenological events can have consequences for the entire ecosystem. Currently, there is a lack of a unified criteria on the methodologies studying phenology and biotic interactions.

2. We performed an extensive integrative review of works evaluating phenology and biotic interactions. We identified four broad categories of studies that have explored biotic interactions within phenology research: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices.

3. We found that spring phenology has received much more attention than any other seasons, while mutualistic and obligated interactions, as well as trophic interactions and networks have been explored more routinely than facilitation or competition. Authors tend to interpret co-existence among species as biotic interactions without any direct measurement of these, particularly in spatial and temporal asynchrony studies, but this also occurs to a certain extent in all categories. We also found a lack of formal examination in most studies exploring phenological mismatches in response to climate change.

4. We propose a conceptual framework for the inclusion of phenology in the study of biotic interactions that apportions research into the conceptualisation and modelling of biotic interactions. Conceptualisation explores phenological data, types of interactions, and the spatiotemporal dimensions, which all determine the representation for biotic interactions within the modelling framework, and the type of models that are applicable.

5. Finally, we identify emerging opportunities to investigate biotic interactions in phenology research, including spatially and temporally explicit species distribution models as proxies for phenological events and the combination of novel technologies (e.g., acoustic recorders, telemetry data) to quantify interactions.

Resumen:

1. Los eventos fenológicos juegan un papel fundamental regulando los servicios ecosistémicos, la naturaleza compleja e interconectada de los ecosistemas conlleva que las interacciones entre diferentes taxones durante eventos fenológicos puedan tener consecuencias sobre el ecosistema en su conjunto. Actualmente no existe un criterio unificado sobre las metodologías de estudio de la fenología y las interacciones bióticas.
2. Hemos desarrollado una revisión integrativa extensiva sobre artículos cuyo objetivo era evaluar fenología e interacciones bióticas. Hemos desarrollado cuatro amplias categorías en las que se pueden agrupar los estudios que han explorado interacciones biológicas en estudios fenológicos: 1) asincronías espaciales y temporales, 2) factores bióticos como covariables, 3) estudios de simulaciones, 4) índices de interacciones.
3. Nuestra revisión muestra que los eventos fenológicos que tienen lugar durante la primavera han recibido mucha más atención que la fenología de ninguna otra estación, así como el hecho de que las interacciones y redes tróficas han sido exploradas más frecuentemente que interacciones de facilitación o competencia. Los investigadores tienden a interpretar coexistencia entre especies como una interacción biótica, sin que haya una medición directa de dicha interacción, en especial en los estudios de asincronías espaciales y temporales, aunque ello también ocurre a cierto nivel en el resto de las categorías. Además, también hemos encontrado una falta de examinación formal en la mayoría de estudios que exploraron desajustes entre eventos fenológicos en respuesta al cambio climático.

48 **4.** Proponemos un marco conceptual para la inclusión de la fenología en el estudio de las
49 interacciones bióticas que divide dicho estudio entre la conceptualización y el modelado de las
50 interacciones bióticas. La conceptualización explora el tipo de datos fenológicos, tipo de
51 interacciones y las dimensiones espacial y temporal, todo ello determina la representación de las
52 interacciones bióticas a lo largo del modelado, así como el tipo de modelos aplicables.
53 **5.** Por último, también identificamos oportunidades emergentes para la investigación de
54 interacciones bióticas en fenología, incluyendo modelos de distribución de especies temporal y
55 espacialmente explícitos usados como representaciones de eventos fenológicos, así como el uso
56 combinado de nuevas tecnologías (por ejemplo: grabadores acústicos o datos procedentes de
57 telemetría) para cuantificar interacciones.

58 **Keywords:** biotic factors, coexistence, mismatch, phenology, species interactions

59 **1. Introduction**

60 Phenology is the study of cyclic and seasonal phenomena in organisms, such as leaf unfolding and
61 senescence, flowering of plants, migration events, and timing of the breeding season (Forrest & Miller-
62 Rushing, 2010; Mayor et al., 2017). The outstanding impacts that phenology exerts in the functioning
63 of ecosystems and their services are well established and have fostered much research in recent
64 decades (van Schaik, Terborgh & Wright, 1993; Peñuelas & Filella, 2001; Peñuelas, Rutishauser &
65 Filella, 2009; Timberlake, Vaughan & Memmott, 2019; Duchenne et al., 2020). Some of these main
66 phenological impacts include the carbon sequestration potential of ecosystems (Le Quéré et al., 2017)
67 with variations in net carbon uptake (Keenan et al., 2014) and carbon regulation (Richardson et al.,
68 2009; Brzostek et al., 2014). Thus, phenology plays a key role in modulating ecosystem processes.

69 The complex and interlinked nature of ecosystems means that changes in the abiotic components
70 (e.g., climate), might alter the cues that phenological events follow (e.g., temperature or
71 photoperiod), which could lead to advanced or delayed phenological events in one or more interactor
72 species (Forrest & Miller-Rushing, 2010). Shifting phenologies among different taxa can display direct

73 or indirect impacts on biotic interactions (Wolf, Zavaleta & Selmants, 2017). For example, earlier
74 flowering time that overlaps with other plant species could expose plants to lower pollinator activity
75 (i.e., direct impact) as a result of competition, while also resulting in reduced herbivory pressure,
76 which has a subsequent effect on fruit onset (i.e., indirect impact) (Vilela, Del Claro, Torezan-Silingardi
77 & Del-Claro, 2018). The sensitivity of biotic interactions and interaction networks to climate change
78 means that many species and ecological networks could experience decoupling or losses of
79 interactions, which could have potentially long-standing consequences for the entire ecosystem and
80 its services (Oliver et al., 2015).

81 The phenological response to climate change drivers has been explored for many taxa, particularly for
82 plants. Earlier flowering and leaf unfolding in spring as a result of climate change are well documented
83 (Primack, Higuchi & Miller-Rushing, 2009; Rafferty & Ives, 2011; Mayor et al., 2017; Mohandass,
84 Campbell , Chen & Li, 2018). However, not all organisms respond in the same way. For example, within
85 a plant community some species might experience noticeably earlier flowering as a response to
86 variations in climatic factors, whereas other species might show low impact or remain unchanged
87 (Vilela et al., 2018). This can result in phenological mismatches at different trophic levels (Fig. 1a,d,
88 e.g. flowering time and pollinator activity; bird migration and insect development), thus threatening
89 biodiversity because of differences in phenological sensitivity to climate (Thackeray et al., 2016;
90 Kharouba et al., 2018). These phenological mismatches have been proven to be particularly important
91 for supressing specialized interactions, where higher trophic levels depend on a reduced number of
92 species in the lower levels (Both, Van Asch, Bijlsma, Van Den Burg & Visser, 2009).

93 The interactions between plant and pollinator are usually asymmetric, where a plant species depends
94 strongly on an animal species (pollinator), but the animal depends weakly on the plant (and vice versa)
95 (Bascompte, Jordano & Olsen, 2006). Asymmetric interactions usually occur within (predominantly)
96 nested networks, allowing both generalist and specialist plants to interact with both generalist and
97 specialist pollinators and thus maintain the ecosystem (Schweigher et al., 2010). Therefore, in the case

of (local or global) extinction of one of the interactors or asynchronies between partners, the network could buffer the effect of such events, but there would be uncertainties related to how resilient species might be to such changes (Fig. 1b,e). Moreover, many species initiate phenological events based on species interactions, with many aphid species initiating migration based on the senescing of host plants (Dixon & Glen 1971; Watt & Dixon 1981), which may or may not be captured by changes in the abiotic conditions alone (Holloway, Kudenko & Bell, 2018). In addition, the effect of climate change can disrupt biotic interactions in many ways, for example, turning from a favourable scenario of facilitation to competitive exclusion or competence (Blois, Zarnetske, Fitzpatrick & Finnegan, 2013) or by advancing or delaying phenology of species that exhibit changes in their interaction types through ontogeny, which is where species shift their relationship from competition to predation, facilitation to competition or herbivory to mutualism during their life cycle (Yang & Rudolf, 2010), illustrated in Fig. 1c,f. Despite the complex network of interactions operating in ecosystems, the role of phenological shifts on species interactions, and vice versa, remain poorly understood (Sargent & Ackerly, 2008; Varpe, 2017). In a recent study, Morente-López, Lara-Romero, Ornosa and Iriondo (2018) documented a great variation of within-season interactions in a plant-pollinator network in which modularity (strength of groups of interacting species) was greatly influenced by species phenology. Thus, evaluating the role of phenology in species interactions is vital for a better understanding of biotic interactions and ecological networks.

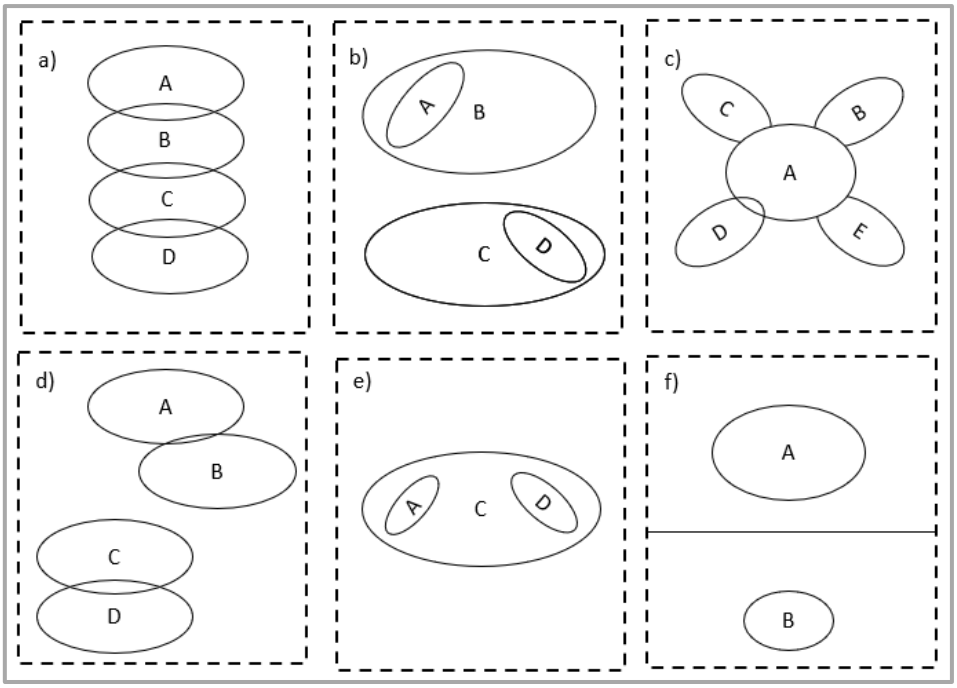

Figure 1. Conceptualisation of biotic interactions under normal conditions, i.e. matching phenologies, among different trophic levels (a,b,c) vs phenological mismatches (d,e,f) caused by an imbalance in the ecosystem, i.e., climate change or fragmentation. a) Species (A, B, C, D) interaction through the trophic network, where A interacts with B, who interacts with C, who in turn interacts with D. b) Representation of obligated interactions (A+B), (B+C) where species A depends on B and species D depends on C. c) Species A favouring through facilitation, under favourable conditions or a particular stage of its ontogeny, by providing nutrients, refugia or resources, the occurrence of species B, C, D and E. d) Interaction decoupling as C and D advanced their phenology while B delayed it and A remained constant as result of a perturbation, i.e. temperature rise. e) A+B interaction lost after a perturbation, i.e. habitat modification or climate change, hence A now depends on C, exerting pressure on both C and D. f) Facilitation turned into competition in where A excluded all species and reduced available space for B through competition.

There are several challenges when incorporating biotic interactions in phenology research, which may have impeded its development. Firstly, there is a lack of information regarding many species interactions, and even when information is available there is often a lack of replication that makes it difficult to extrapolate the methodologies and results across species, environments, and models (Baselaga & Aráujo, 2009). The high complexity of biotic interactions and the mechanisms involved in the build-up of interaction networks, makes it difficult to model them statistically, being typically parameterised in models as proxies of presence-absence of interactor partners (Palacio & Girini, 2018). Similarly, many interactions are unknown, hindering evaluation of biotic interactions for many species (Atauchi, Peterson & Flanagan, 2018; Morente-López et al., 2018), and furthers the use of

subjectively defined proxies. Finally, biotic interactions are also dynamic in nature; however, they have typically been evaluated during just one part of the life cycle (e.g., spring), assuming that interactions are static in space as well as time (Bateman, Van Der Wal, Williams & Johnson, 2012).

Therefore, biotic interactions have been relatively neglected in phenology research (Elzinga et al., 2007; Morente-López et al., 2018) despite the important role they play in life cycle events. Consequently, developing a generalised framework for the incorporation of biotic interactions in phenology research has been difficult, meaning studies addressing interactions among different species and trophic levels are rare. While methods have been proposed to investigate species interactions in phenology research, these have often arisen in disparate fields, with a predominant focus on quantifying temporal mismatches in relation to the abiotic conditions. By not implementing measures of biotic interactions in phenology research, models ignore one of the most important ecological processes that can modify, disrupt, or decouple phenological events across ecosystems.

In this review we aim to investigate the methodologies used to evaluate the effect of phenological change in biotic interactions and address the main challenges derived from the study of these complex relations. This review aims to identify important gaps of knowledge, explore different approaches of studying biotic interactions within phenology research and provide future directions, all pivot questions for integrative reviews (Sayer, 2018). Details of the methodology used to undertake the review and the list of studies within an initial Web of Science keyword search are presented in Supplementary Information 1. Studies that have explored biotic interactions within phenology can be broadly grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices. Through this we review, we aim to create a generalised framework for the incorporation of biotic interactions in phenological research. Finally, we end our review by exploring emerging opportunities that could be employed to investigate biotic interactions within phenology research, and subsequent challenges arising from these new methods.

2. Spatial and Temporal Asynchronies

Asynchrony among species in phenology research has predominantly focused on variations in climatic factors (e.g., temperature, precipitation) that are the common drivers of phenological events of many taxa, consequently leading to spatial and temporal mismatches between interlinked species (Yang & Rudolf, 2010; Thackeray et al., 2016; Mayor et al., 2017). Most studies investigating temporal mismatches in phenological events have focused on monitoring climatic induced changes of a single species or an array of species over an extended temporal period (e.g., 30 years) that are usually linked through the trophic network (Gordo & Sanz, 2006; Jones & Creswell, 2010; O'Neil et al., 2012; Dunn & Moller, 2014). For example, fluctuations in bird migration trends, arrival dates, and laying dates have all been documented in relation to decades of variation in temperature and precipitation in wintering grounds and spring breeding areas (Gordo & Sanz, 2006; Jones & Creswell, 2010; Dunn & Moller, 2014). However, studies typically rely on the assumption that earlier emergence or arrival to breeding grounds will result in the mismatch of interactions that are not evaluated or quantified in any way.

Advancements on incorporating biotic interactions within studies investigating temporal mismatches have systematically modelled the relationship between species (Gordo & Sanz 2005; Burkle, Marlin & Knight, 2013). For example, Gordo and Sanz (2005) used a temporal series of phenological events of plants and pollinators including date of flowering and pollinator emergence over a 50-year period in order to infer decoupling of plant-pollinator interactions. Climate induced changes in plant phenology were estimated using dimension reduction models (e.g., two dynamic factor analyses) to identify common temporal patterns within plant phenological events. Advancing on this, the authors employed regression analyses to determine patterns of change on the timings of phenological events (e.g., insect emergence, bird migration) showing advancement on insect emergence related to advanced flowering but the interaction among both was not explicitly analysed. Figure 2a highlights a hypothetical visualisation of such results, with the fitted line representing a linear model for showing

185 the trend on timing (asynchronies) of two phenological events, plant flowering and insect emergence.
186 The dotted line represents documented differences in Julian days between the two studied
187 phenological events, extracted from independent datasets, and evidences the lack of direct method
188 for the evaluation of biotic interactions in previous research.

189 Biotic interactions are frequently inferred as species co-occurrence in time rather than documenting
190 them directly in the field. However, Rafferty and Ives (2011) evaluated the timing of flowering blooms
191 using t-tests to determine significant advancements on flowering over time, categorising plants into
192 two groups; advanced flowering and unchanged due to climate change. By recording presence of
193 flowering and visitation, they tested whether phenological mismatches among plants and pollinators
194 could be a limiting factor on pollination for both groups of plants. Visualisation of these records using
195 a contingency table (Fig. 2b) provides a clear representation of which species are (significantly)
196 mutualistically interacting.

197 Thus, temporal mismatches in phenological events are frequently used as proxies of biotic
198 interactions, i.e. egg laying date and peak abundance of main food source as proxies for predator-prey
199 interactions (Visser, Holleman & Gienapp 2006; Mayor et al., 2017). Usually those changes in
200 phenology or interactions are then statistically tested by the application of linear regression models
201 where the explanatory variables are the interaction between two species, measured as the
202 coexistence of interactor partners over time and space, i.e. presence or absence of species A and B in
203 a place during a particular time period, or a phenology event of one or more species. For example,
204 studies have regressed differences in the timing for which phenological events of mutualistic or
205 obligated interactors occur during a given period (Hegland, Nielsen, Lázaro, Bjerknes & Totland, 2009;
206 Saino et al., 2009; Rafferty & Ives 2011; Bartomeus et al., 2011). For instance, Mayor et al. (2017)
207 investigated how the phenological intervals between green-up and bird migrant arrival changed for
208 48 breeding passerine species in North America, identifying both positive and negative changes in
209 phenology (Fig. 2c). Interestingly, they highlighted instances where positive values of the phenological

interval were given because migrants arrived earlier, tracking advances in vegetation phenology. Conversely, negative values in phenological intervals corresponded to migrants showing advanced or unchanged phenology while vegetation phenology was delayed. Surprisingly, they found that even when migrants arrived earlier following trends in green up, they did not keep pace adequately with it. Additionally, the phenological interval varied throughout ecoregions, suggesting the important role geography may play in phenology.

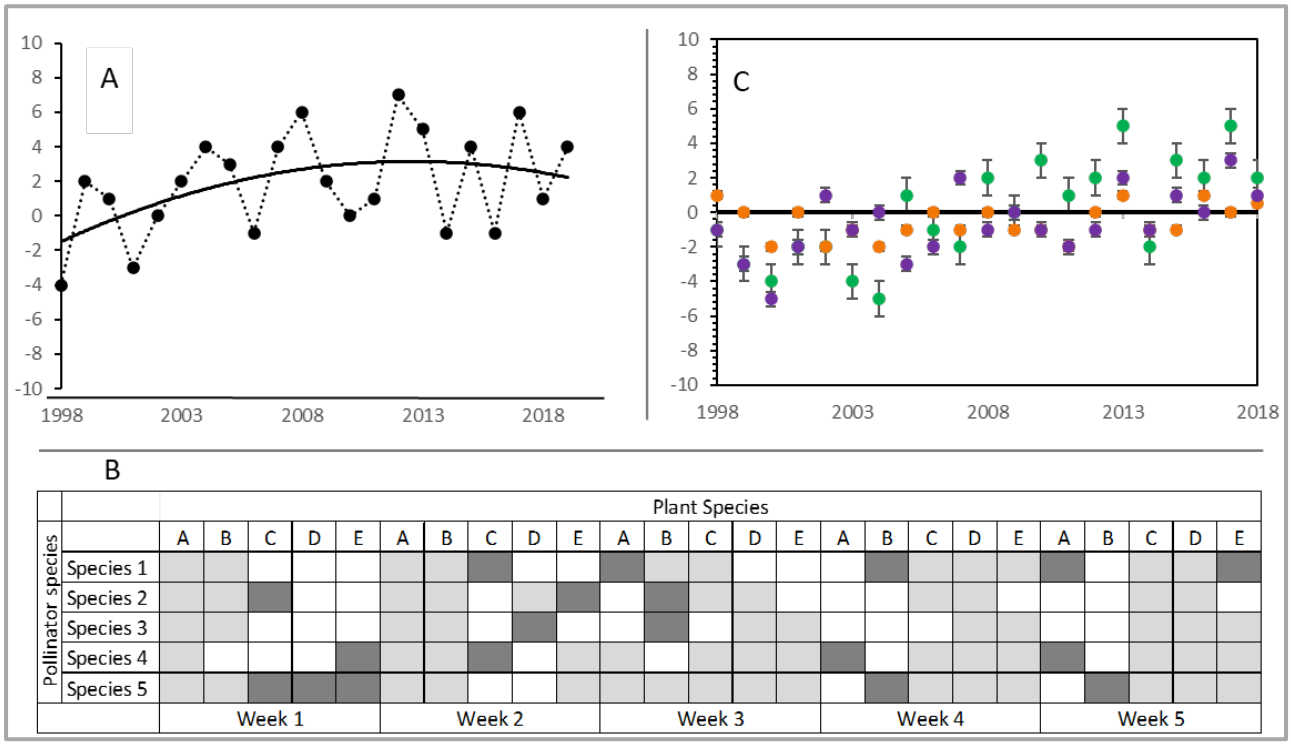

Figure 2. Different approaches to modelling biotic interactions from proxies. A) Modelled elapsed days between date of insect emergence and flowering date for an insect and its main flower resource, showed in calendar days (Y axis), over a decade (X axis), adapted from Gordo and Sanz (2005). Black dots represent positive or negative differences between timing on phenologies of the two taxa, dotted line reflects trends in variations of temporal asynchronies, fitted line represents a linear model of the tendency of these asynchronies. B) Conceptualization of an experimental network of plant-pollinator interactions over time in which an assemblage of plants (species A, B, C, D and E) was manipulated to evaluate the role of changed vs unchanged flowering timing, adapted from Rafferty and Ives (2011). i.e. A, and B manipulated to flower earlier than their current mean flowering date, C and D manipulated for a delayed flowering and E remained unchanged according its current flowering date. Pollinator visits (species 1 to 5) are documented over time, light grey squares represent plant-pollinator interactions and dark grey squares represent low rate pollinator visitation. C) Trends of phenological change, in comparison to mean (0), estimated by number of calendar days per year (Y axis) for three phenological events: green up (green dots), date of arrival of a migrant bird species (orange dots) and date of an insect emergence (purple dots), over a decade (X axis), bars indicate standard error.

Phenological advance corresponds with positive values over the mean while delay in these events are represented by negative ones, adapted from Mayor et al. (2017).

Application of temporal asynchronous analysis requires long-term time-series data, and due to the resources required to collect such data, this research is often restricted spatially to very localised sites. Subsequently, studies are beginning to use species distribution models (SDMs) to quantify spatial and temporal asynchrony in phenology. SDMs use information regarding the locations of organisms together with geospatial environmental parameters to identify species-environment relationships and use these to extrapolate habitat suitability into novel space and time (Elith & Leathwick, 2009). While phenology has not been a traditional application of SDM research, in part due to their static representation of a species niche (Peterson et al., 2011), studies are beginning to emerge (Porfirio, Harris, Stojanovic, Webb & Mackey 2016; Yun, Lee & Yoo, 2020). For example, Yun et al. (2020) modelled the distribution of the cuckoo (brood parasite) and 12 passerine birds (host species) to ascertain the amount of spatial overlap in their distributions under changing climates. By quantifying the difference in spatial area, the authors identified a decrease in suitable habitat for all species, but also a decrease in the amount of overlap between cuckoos and their hosts, subsequently impacting breeding phenology.

Therefore, the need for a spatial consideration in any phenological research investigating asynchrony among species is key, as changes in timing may occur differently across ecoregions, ranges, and altitudes. For example, Benadi, Hovestadt, Poethke and Blüthgen (2014) used an altitudinal gradient as proxy for expected climate change over time, to evaluate the degree of synchrony between specialised flower visitors and their main plant resource. By modelling plant-insect phenological shifts among different altitudes with linear mixed-effects models, the authors demonstrated that consistency of specialised pollinators and phenological synchrony with their main source was not maintained at different altitudes.

Studies investigating spatial and temporal mismatches among species have generally focused on spring phenology (Visser et al., 2006; Primack et al., 2009; Mayor et al., 2017; O'Neill et al., 2012;

Bartomeus et al., 2011; Phillimore, Leech, Pearce-Higgins & Hadfield, 2016), while studies addressing autumn phenology are scarcer (Gordo & Sanz, 2005; Gordo & Sanz, 2006; Gallinat, Primack & Wagner, 2015). Although evidence of advanced spring phenology is widespread (Heghland et al., 2009; O'Neill et al., 2012; Phillmore et al., 2016), this trend is unclear for autumn phenology and the lack of comparative studies makes it difficult to discriminate patterns during this season (Gordo & Sanz, 2005). Moreover, in many of the aforementioned studies, interactions were considered to be static among species, as well as expected to change linearly with the abiotic conditions. The expected linear change in such cases is realistic until some point, but species will not advance their phenology endlessly. Thus, the nature of relationships, such as type and strength, might change along with abiotic conditions, meaning the selection of parameters need to be appropriate to the system under study in order to account for such factors (e.g., non-linear relationships - Austin, 2007). Consequently, under the current climate change scenarios (IPCC, 2018), phenological mismatches have the potential to deeply impact biotic interactions, therefore long-term spatially and temporally explicit phenological studies could help to improve management actions to preserve the integrity of interaction networks.

3. Biotic Factors as Covariates

Despite their relevance, biotic factors have been relatively neglected in phenological studies, particularly when compared to the historical use of abiotic drivers (Thackeray et al., 2016; Wolf et al., 2017); however, studies have begun to incorporate them as additional explanatory variables or covariates in statistical models. Biotic variables are often included in the models to investigate the role of species interactions on phenological events, predominantly using data obtained from manipulative field studies (e.g., visual identification among transects, capture-recapture, and monitoring of nests - Visser et al., 2006). Generally, interactions through trophic levels are documented more often since impacts on one of the interactors of these obligated or specialised networks, in which one species directly depends on other as a food source, will lead to a response on the other partner. For example, by evaluating differences in the onset of forage species (either herbivores or predators), the impact

279 of any phenological mismatch in the reproductive success of forager populations can be estimated
280 (Visser et al., 2006; Post & Forchhammer, 2008). These manipulations aim to account for the effect of
281 temporal or spatial changes in environmental conditions, phenological events or biotic interactions.
282 For example, Martin and Maron (2012) tested the effect of reduction in snow cover, given a 25-year
283 period of snowfall decline, as a factor influencing bird and plant population declines through increased
284 herbivory and nest predation. The authors studied changes in plant assemblages for herbivory-
285 prohibited (i.e., simulated snow cover) and herbivory-exposed sites finding that reduction in snow
286 cover exposed plant assemblages to higher herbivory pressure, leading to declines in bird populations
287 due to increased nest predation. However, an increase in plant and bird populations (including a
288 reduced nest predation) was documented in herbivory-prohibited areas.

289 Research has also addressed the importance of the spatial dimension of phenological shifts. For
290 example, larger shifts in phenology (e.g., longer mismatches in Julian days) have been related to higher
291 latitudes and elevations, which act as a proxy for increases in global temperature (Chmura et al., 2019).
292 Altitudinal gradients serve to illustrate climate change effects as conditions in upward populations are
293 usually associated to pre-climate change scenarios while downward populations serve as example of
294 the conditions that upward populations would experience in the future (Alexander, Diez & Levine
295 2015). Although some of the reviewed studies monitored biotic parameters, there is still a marked
296 importance of abiotic factors, with studies typically testing several within models i.e. factors such as
297 temperature increase and nutrient enrichment on specialised trophic interactions (Lu, Siemann, Shao,
298 Wei & Ding, 2013; de Souza Laurindo, Gregorin & Tavares, 2017; Terraube, Villers, Poudré, Varjonen,
299 & Korpimäki, 2017). For example, Terraube et al. (2017) showed the importance of climate factors and
300 forest management on the foraging success of an owl species by using field data and GLMMs. The
301 authors documented a trend of decreased prey biomass stored in nests related to increasing rainy
302 days and days with frost, which in turn is expected to affect the biomass and fitness of the target owl
303 species. However, despite the importance of incorporating both abiotic and biotic factors on
304 interactions, few experimental studies have actually tested this within a phenology context.

Alexander et al. (2015) exposed plants to different treatments of abiotic conditions and presence of expected interactor species in order to determine if competition or facilitation would dominate plant assemblages under predicted climate change. By using mixed-effect models and GLMs, the effect of presence of competitors on the transplanted individuals was estimated, showing that under warmer conditions the identity of the competitor had a significant effect on the transplanted individuals' success. Wolf et al. (2017) carried out experiments manipulating biodiversity of plant assemblages to reflect random or realistic biodiversity loss, in terms of the number and identity of species. Their aim was to test for the effect of biotic interactions on the timing of flowering peak (highest flower abundance per species and plot were used as a surrogate variable for time of flowering) of each species. In this case, plots with low plant diversity showed earlier flowering, while flowering peaks between species were more dispersed in high diversity treatment plots than in monocultures. Other studies have begun to test both abiotic and biotic factors in experimental settings (Bresson, Varoquaux, Bontpart, Touraine & Vile, 2013; Koyama & Tsyuzaki, 2013), with studies manipulating environmental conditions useful to determine changes in phenology and the evolution of specialized interactions under predicted climate change conditions. Moreover, experimental works manipulating abiotic and biotic conditions in order to evaluate phenological response and adaptive success are performed by translocating individuals (usually plants) to new areas (within and beyond) their distributional range, or through lab manipulation (Lau & Lennon 2012). Thus, the inclusion of biotic interactions in phenology research could change the statistical response, effect, and importance of abiotic variables.

Despite these advancements, many studies lack any direct measurement of biotic interactions. For example, Merrill et al. (2008) documented the distributional range shift of a butterfly related to elevation on its lower distributional limit and to the absence of host plants at their upper distributional limit. Since the target butterfly needed the presence of any of the host plants for completing different stages of their life cycle (i.e., phenology), the lack of host plants at higher elevations was assumed to be responsible for determining the butterfly's upper distributional limit, despite there being no direct

measurement of their biotic interaction, taking host plant presence as a proxy. Similarly, Kass et al. (2020) used presence of resource and refugia providing plants at a monthly resolution, aiming to capture the importance of plant phenology on the distribution of the monarch butterfly during autumn migration, with co-existence records serving as a proxy to infer suitable habitat for the butterfly.

Conversely, there is usually a lack of replication in most field or manipulative studies. For example, even when biotic interactions are statistically proven to be one of the main explanatory variables within a system, the lack of replication over time and the scarcity of comparative studies might lead to misinterpretations. For instance, Theobald, Gabrielyan and Hillerislambers (2016) demonstrated the importance of pollinator-mediated seed production of a montane plant species. The authors tried to investigate the role of pollinators for determining the range limit of the plant (through pollen limitation), suggesting the importance of different pollinator groups for reproductive success; however, factors determining the species' range limit could not be separated from plant interannual variations. Further, some studies evaluate small populations which highlight the fact that small sample sizes might mask the effect of other possible factors and lead to erroneous interpretations (Post & Forchhammer, 2008; Benadi et al., 2014). Furthermore, although most of these experimental studies include environmental variables, given the scale and dimension of these open mesocosm experiments, there might be environmental variables that are not considered and could explain some of the statistical variation found in them (Wolf et al., 2017), compounding our ability to interpret such biotic interactions within these models. In addition, most of the studies address spring phenological events monitoring weather conditions during the growing season neglecting winter climate change conditions that are of great importance for the phenology of plant and pollinators (Makoto et al., 2014).

4. Simulation models

Simulation models are statistical models where one or more parameters are manipulated in order to elicit predictions in the response of the ecological factor under consideration (Chuine & Régnière, 2017). These factors could include the presence or abundance of a species, the spatial or temporal changes of a particular phenological event, and the persistence of a biotic interaction. These models have been used to explore a wide array of phenological events, such as co-occurrence of interactor species influencing pollination interactions (CaraDonna et al., 2017), the role of plant-pollinator synchrony in community assemblages (Bartomeus et al., 2013) and the role of changing phenology on population trends (Dunn & Moller, 2014). Although simulations exploring the responses of species under climate change are common in ecology (Keith et al., 2008; Virkkala, Heikkinen, Leikola & Luoto, 2008; Dullinger et al., 2012), during the development of this review we found very few papers where simulations investigated the effect of climate change on phenological events or biotic interactions (Memmott, Craze, Waser & Price, 2007; Araújo, Rozenfeld, Rahbek & Marquet, 2011; Roberts, Tansey, Smithers & Phillimore, 2015; Bateman et al., 2016; Goberville et al., 2016; Schleuning et al., 2016).

Simulation models have been used to predict the evolution of ecological networks, by modelling predicted phenological mismatches among interactor partners, as well as extracting interactor species from modelled networks to determine extinction effects when one or more species are removed (Memmott, Waser & Price, 2004; Memmott et al., 2007). By modelling extinctions in mutualistic networks, species sensitivity to climate change driven coextinctions can be estimated. For example, Schleuning et al. (2016) modelled the effects of climate change on ecological networks, and subsequently simulated secondary species extinction as a consequence of the sequential loss of plant and animal species. Network sensitivity was then quantified ranging from no secondary species going extinct to all species. Simulations showed that specialized animals would suffer greater impact than plants from secondary extinctions in mutualistic networks due to climate change. Moreover, applications of simulation models can be used to construct networks of co-occurrences that serve as

proxies of interactions or to infer biotic interactions from co-occurrence patterns (Araújo et al., 2011; Araújo & Rozenfield, 2014). For instance, Araújo and Rozenfield (2014) created a point-process model from co-occurrences to infer biotic interactions and to evaluate their relevance at different spatial scales. Spatial overlap (attraction or repulsion) together with probability of occurrence of interactors in space was interpreted as a signal of biotic interactions that were scored according to the number of times species co-occurred within cells in order to estimate their spatial importance. Their results suggested that the effect of negative interactions was clearer at fine scales and diluted at coarse scale whereas positive interactions (mutualism, commensalism) and those related to consumer-resources were scale independent.

Simulations have also been useful to model species distributional limits and probability of survival beyond geographical ranges. For example, Benning, Eckhart, Geber and Moeller (2019) used field experiments to train simulations on plant fitness in the presence and absence of herbivory. Simulations were tested by exploring the impact of herbivory on the fitness and survival of a Californian annual plant species, investigating delayed phenology and the probability of survival beyond its geographic range. When climate conditions were advantageous (i.e. higher precipitation) simulations showed that probability of survival and fitness of the species at their range limit and beyond was much higher when the effect of herbivory was moderate than when this antagonistic biotic relationship was excluded, although not high enough to support population establishment and growth. While this study explored antagonistic interactions, mutualistic interactions within networks, such as pollination, were addressed the most frequently across all simulation studies (Memmott et al., 2004; 2007; Bartomeus et al., 2013; Schleuning et al., 2016).

Few studies employed mechanistic models such as physiologically based weather-driven demographic models (PBDMs) aiming to incorporate phenology and biotic interactions while also accounting for abiotic parameters and multitrophic population dynamics (Ponti, Cossu & Gutiérrez, 2009; Ponti et al., 2013). Further, recent approaches using simulations to explore phenology have shown that such

models can be used to predict the probability of detecting pairwise biotic interactions through the use of occurrence data and detectability of species, estimation of probability of interactions, and connection of interaction networks (Graham & Weinstein, 2018).

However useful simulations are, these approaches face similar challenges, such as the lack of robust data on interaction networks, as well as sensitivity to the lack of knowledge about rare interactions (Olito & Fox, 2015). In many cases, the lack of basic knowledge on species biology and biotic interactions could lead to erroneous predictions or interpretations that under- or over-estimate the power of these models (Memmott et al. 2007). Additionally, considering a network of interactions as a sealed system is often a caveat of these methodologies. For example, when modelling species extinctions, these models are performed assuming that no new interactions are entering the system, which can undermine the power of the model as this is not entirely realistic. Moreover, despite the importance of phenology structuring networks of interactions (Morante- López et al., 2018), studies modelling biotic interactions frequently ignored the phenological dimension of these (Araújo et al., 2011; Araújo & Rozenfield, 2014; Schleuning et al., 2016). Although there are some advances in the field of predictive models of biotic interactions, in particular the novel approach of Graham and Weinstein (2018) to develop models predicting species interactions, the lack of a robust methodology on this topic limits the use to elaborate predictions on species interactions.

5. Interaction Indices

Interaction indices have been used to measure the degree of interaction among species, with research focusing on synchrony among interactor species (Donoso, Stefanescu, Martínez-Abraín & Traveset, 2016; Oleques, Overbeck & de Avia, 2017), interactions within communities (Buxton, Brown, Sharman, Gabriele & McKenna, 2016; Molina-Venegas et al., 2016; Oliver et al., 2018), and interactions as a network (Junker et al., 2013; Robinson, Losapio & Henry, 2018). For example, Benadi et al. (2014) evaluated local specialisation of insect on flower morphology, calculating two indices (d') and (H2') to estimate the level of specialisation on pairwise and interaction networks, respectively. Both indices

compared the number of visits of a pollinator (later pooled to taxonomic groups) to a plant species, and then further comparing visits to total flower resources and a null model of expected visits. The authors demonstrated different degrees of specialisation among taxonomic groups of pollinators and the importance of floral traits (tube length) rather than plant species identify.

Novel advances on field monitoring of phenology, particularly using new technology, are leading to the development of community interaction indices (Buxton et al., 2016; Oliver et al., 2018). For example, Buxton et al. (2016) used a novel acoustic index, developed by Pieretti, Farina and Morri (2011), to monitor spring and winter phenology of songbirds. The acoustic complex index (ACI) measures the vocalizations produced on an avian community and poses as an important tool for the study of phenological events at large spatiotemporal scales. This index is calculated as the differences in sound pressure level among adjacent seconds of the recorded period divided by the total value of sound pressure level for the recorded band. Acoustic recorders were placed in different areas in order to acquire different ACI values over a three-year period. ACI values were compared with species-specific acoustic analyses to determine changes in the acoustic landscape produced by the arrival of migrant birds. Further, the relationship between species beta-diversity and ACI was documented with differences in values among seasons calculated through Bayesian change point analyses and GLMMs. Abrupt changes in phenology were recorded in spring, but these were not as prominent during the autumn season, partially due to extreme weather events obscuring the acoustic data. Thus, potential of acoustic recorders to continually monitor the phenological landscape offers a unique insight in measuring how phenology (and subsequent biotic interactions) change over time (Deichmann et al., 2018), and while several novel challenges are associated with the technology (Shonfield & Bayne, 2017) their use offers a means to establish a holistic monitoring system that can integrate both local and global data to phenology research (Buxton et al., 2016).

Junker et al. (2013) investigated plant pollinator networks using two interaction indices to account for functional individual traits (S_i) and multiple traits (V_i) structuring pollinator niche-breadth while also

456 evaluating the effect of plant phenology. They expected that individual flower traits of different plants
457 visited by the same taxon would have lower Euclidean distance between them than those that do not
458 share visitors. To investigate this hypothesis the authors calculated the individual trait width index (S_i)
459 that employed distance matrices, weighted means, and random distances (among other parameters).
460 Simultaneously they created the trait volume index (V_i) exploring groups of flower traits that could
461 influence pollinator preferences, calculated as the product of all individual S_i of each tray by each
462 volume V_i for each taxon as a measure of taxon specialisation. The authors demonstrated that
463 specialist pollinators showed no restrictive morphological traits to access nectar resources and were
464 influenced by plant phenotypes, whereas generalist pollinators showed no preferences across a suite
465 of traits.

466 **6. Proposed conceptual framework**

467 Phenology has developed within disparate fields, including ecology, geography, physiology, chrono-
468 biology and genetics, meaning there has been a wide variety of viewpoints in how to address this
469 phenomenon (Visser, Caro, van Oers, Schaper & Helm, 2010; Pau et al., 2011). Moreover, biotic
470 interactions are complex; they change over time, assemble and decouple by processes such as
471 turnover, and depend on many factors such as modularity (strength of sets of interactions), climate
472 change, local extinctions and presence of invasive species (Schweiger et al., 2010; Schleuning et al.,
473 2016; CaraDonna et al., 2017; Morante-López et al., 2018). In addition, interaction type, strength, and
474 effect (positive or negative) is expected to vary with species ontogeny (development of organisms
475 within their lifespan), for example, herbivores turning into pollinators or alternating predation-
476 competition. Thus, including the broad scope of interactions within the lifespan of species would be
477 more accurate than focusing on seasonal ones (Yang & Rudolf, 2010). Despite some efforts to provide
478 frameworks for the study of phenology (Visser et al., 2010) and the shifts of phenology-ontogeny (Yang
479 & Rudolf, 2010), there is a need to define a common framework for research addressing biotic
480 interactions within phenology. Here we propose a framework for the inclusion of biotic interactions

481 within phenology (Fig. 3), apportioning this into two interconnected factions where research is aimed
482 towards 1) conceptualising biotic interactions and 2) modelling biotic interactions.

483 Conceptualising the biotic interactions within phenology depends on the data, type of interaction, and
484 spatiotemporal dimension of the research. As identified throughout this review, there has been a wide
485 range of data used, including Julian day of phenological events and the presence and/or abundance
486 of species at a given location. This data represents various inter- and intra-species interactions that
487 include information on facilitated, obligated, and trophic relationships. Finally, the temporal and
488 spatial dimensions of these data and interactions are imperative for the methodologies implemented,
489 as this determines whether research focuses on a particular moment of the life cycle of a species or
490 across an extended time period (Yang & Rudolf, 2010). All this information is fundamental for
491 specifying whether the biotic interaction is measured directly through field or experimental research
492 or indirectly through the use of biodiversity proxies or co-existence records.

493 The consideration of co-existence as a biotic interaction or as a proxy of a biotic interaction has
494 received a renewed discussion among ecologists recently (Dormann et al., 2018; Blanchet, Cazelles &
495 Gravel, 2020; Peterson, Soberón, Ramsey & Osorio-Olvera, 2020). In the recent review by Blanchet et
496 al. (2020), the authors emphasise that co-existence records are a poor proxy for biotic interactions,
497 providing a detailed discussion arguing that very extensive (and rarely available) datasets would be
498 needed to test this, but more importantly the biotic interaction must exert a greater signal before it
499 can be inferred within co-existence records. Building on this foundation and the research incorporated
500 in this review, we agree with the premise and propose that studies that use historical temporal
501 datasets of multiple individual species or spatial datasets of multiple species presence-absence must
502 be considered co-existence studies rather than biotic interactions. This is due in part to the fact that
503 these studies often have different data collection methods for taxa and seldom directly record
504 interactions in the field. When coupled with the limitations identified in the statistical models in
505 section 2 (e.g., Austin, 2007), any signal of biotic interaction must be treated with caution.

Modelling of biotic interaction or co-existence is dependent on the variable representation. We have identified three common categories of variable representation; a) activity length (e.g., Julian days or mismatch indices - Mayor et al., 2017), biodiversity parameters (e.g., presence-absence, abundance, functional traits, richness gradients) and c) interaction rates (e.g., herbivory rate, predation rates, etc.). We have also identified that research addressing biotic interactions within phenology often considers the importance of abiotic factors. Subsequently, there is often a need to select both, which includes the type of abiotic parameters relevant to the question at hand. Selection of abiotic parameters is well established in phenology, but it remains important to consider the representation of variables (e.g., mean, max, min) and the appropriate spatial and temporal resolution (van de Pol et al., 2016; Holloway et al., 2018; Simmonds, Cole & Sheldon 2019). From these variables, the modelling approaches identified through Sections 2-5 should then be selected according to the most appropriate data, interaction, spatiotemporal dimension, and biotic representation. Importantly, not all representations are suitable for all methods, highlighted in Fig 3. Such a framework should foster discussion among researchers investigating co-existence and biotic interactions within phenology research and provide signposts for researchers aiming to begin initial work in this discipline.

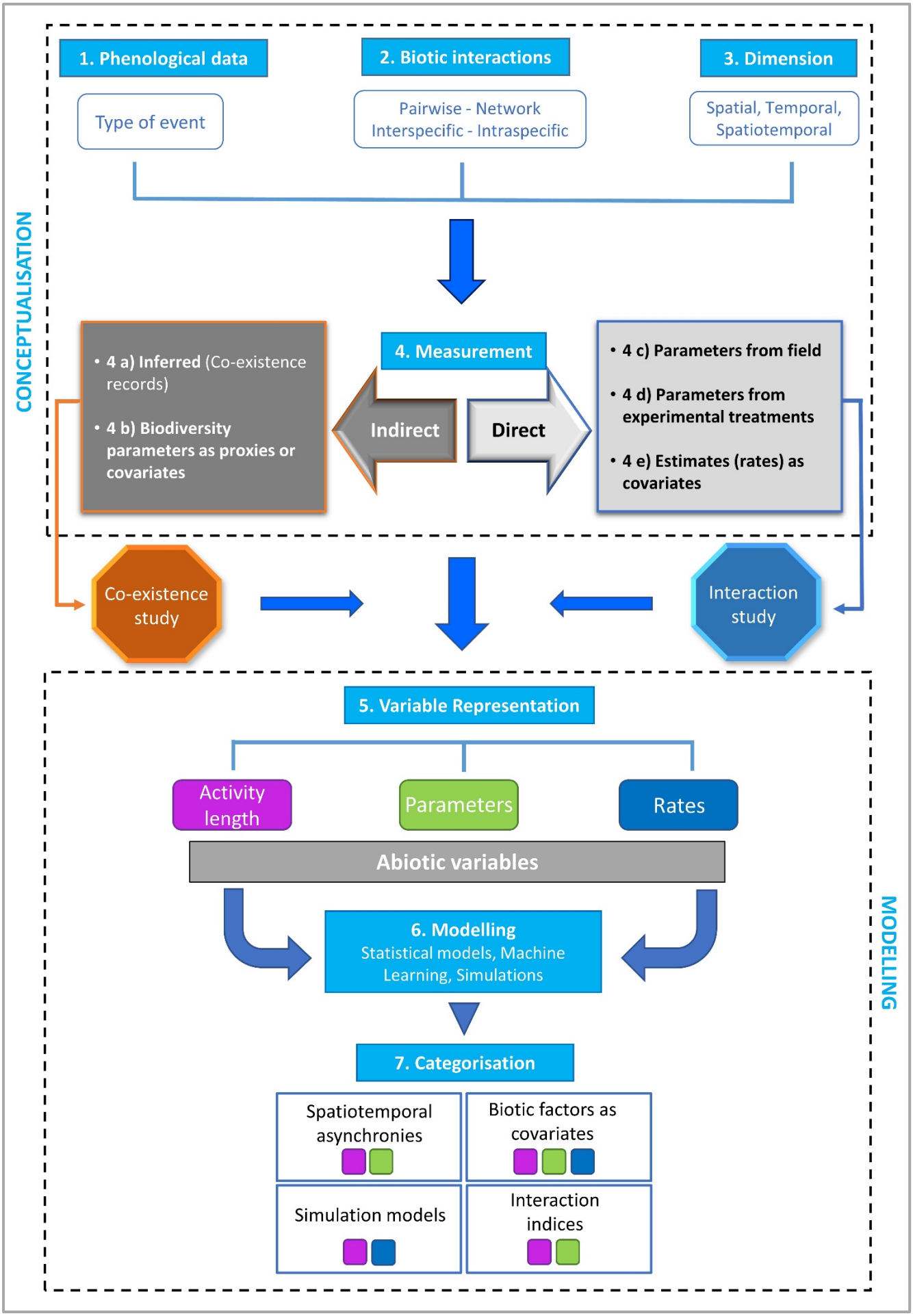
CONCEPTUALISATION
1. Phenological data
Type of event
2. Biotic interactions
Pairwise - Network
Interspecific - Intraspecific
3. Dimension
Spatial, Temporal, Spatiotemporal
4. Measurement
Indirect
Direct
• 4 a) Inferred (Co-existence records)
• 4 b) Biodiversity parameters as proxies or covariates
• 4 c) Parameters from field
• 4 d) Parameters from experimental treatments
• 4 e) Estimates (rates) as covariates
Co-existence study
Interaction study
MODELLING
5. Variable Representation
Activity length
Parameters
Rates
Abiotic variables
6. Modelling
Statistical models, Machine Learning, Simulations
7. Categorisation
Spatiotemporal asynchronies
Biotic factors as covariates
Simulation models
Interaction indices

Figure 3. Framework illustrating the conceptualisation and modelling of biotic interactions in phenology research. Conceptualisation occurs during points 1 to 4, in which researchers need to identify the type of event (1), which refers to the phenological event of study, e.g. flowering time, emergence time, first flight, bud burst, etc., then the interactions of interest (2), e.g., pairwise or network, inter or intra-specific, and type of interaction i.e. trophic (herbivory, predation, etc.), positive (facilitation, mutualism, commensalism), negative (competence, amensalim) or neutral. Then researchers must consider the dimension (3) of study, which accounts for the different spatial and temporal extent of the variables that will shape the modelling process. Finally, this will lead to the measurement of biotic interactions (4), in which we discriminate between indirect (4a-b) and direct (4c-e) measurements. Indirect measurements include those that have been quantified from co-existence records (4a) or parameters that use proxies or covariates (4b), including presence-absence and functional traits. Direct measurements include parameters directly monitored in the field (4c), including pollinator visitation, parameters from experimental treatments (4d), including manipulated vs non-manipulated individuals, and estimates (rates) as covariates (4e), including predation or herbivory rates. We propose that indirect measurements should proceed as co-existence studies, while direct measures should proceed as interaction studies. The modelling of biotic interactions and co-existence studies occurs during points 5-7. There are three main ways in which the study variables are often represented (5): Activity length (purple box) i.e. differences in arrival date, emergence date, flowering time, typically measured in Julian or calendar days. Parameters (green box), when variables of study are ecological measurements such as richness, functional traits, distribution of interactors, presence - absence data, etc., and Rates (blue box), when the variables are estimated as a measurement of a biotic interaction, e.g. predation rate, parasitism rate, pollination success. The selected variables together with the abiotic variables of interest are then modelled (6) using the approaches applicable for the study of biotic interactions, leading to (7) the four identified categories where coloured quadrats (purple, blue and green) in the lower box symbolize the type of variable representation typically incorporated in the different modelling approaches.

7 Emerging Opportunities and Challenges

7.1 Spatial Modelling through SDM

Accounting for the complexity that phenological events pose at both spatial and temporal scales is difficult. With advances in data collection, SDMs (as described in section 2) are now being parameterised more readily with temporally explicit variables (e.g., normalized difference vegetation index (NDVI) for the date closest to the timestamped species observation). This removes some of the uncertainty in projecting seasonal distributions (Holloway & Miller, 2017), with the distribution projections being used as estimates for phenological events. For example, Gschweng, Kalko, Berthold, Fiedler, and Fahr (2012) matched telemetry data with meteorological and habitat data to project monthly distributions of the Eleonara's falcon in Madagascar, identifying seasonal patterns of distributions, and relating this to the timing of migration events. Distribution projections could

theoretically be generated at finer (e.g., daily, weekly, or monthly) timescales, which may capture important information regarding the relationship between phenological events and species distributions. Figure 4 provides an illustrative example of SDM projections for the migratory barn swallow within the island of Ireland parameterized on spatially and temporally explicit observations and environmental data. The increase in habitat suitability for barn swallows in April aligns with their migration, and supports the premise that SDMs parameterised on averaged climate variables (e.g., mean temperature) have often failed to capture the actual variability that species experience in short time periods which drive changes in the spatial distributions across the life cycle (Eyre, Rushton, Luff & Telfer, 2005).

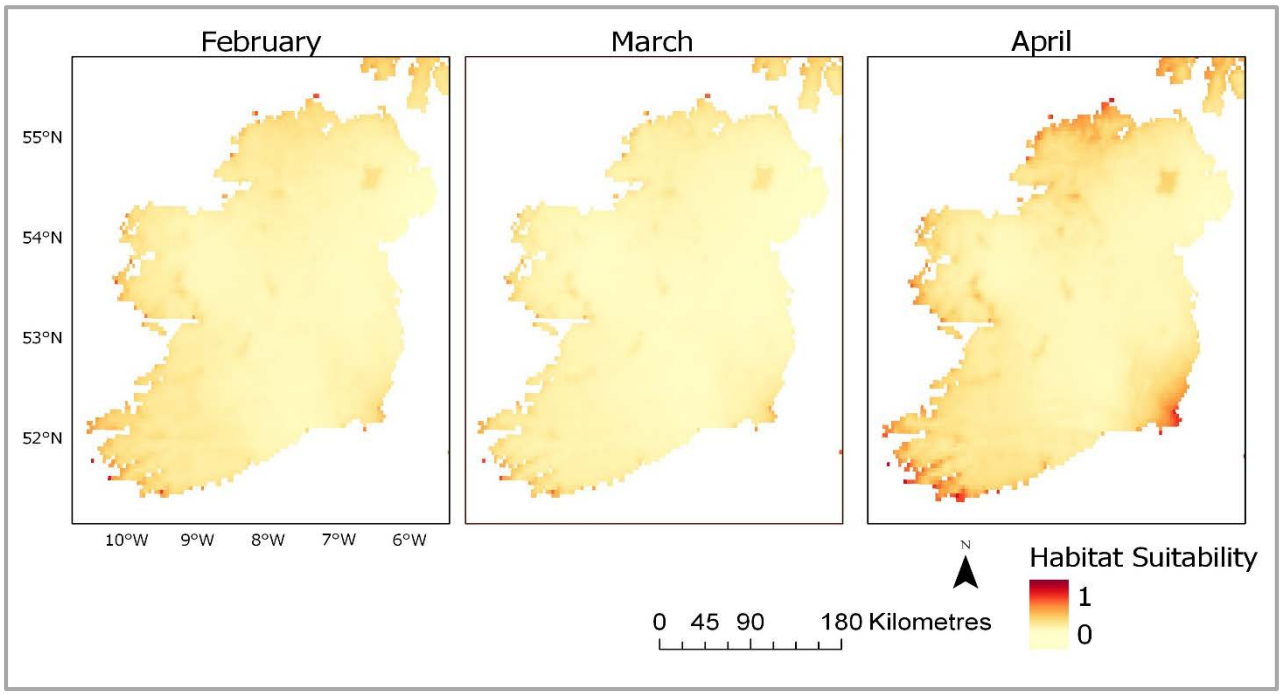

Figure 4. Example of monthly habitat suitabiltiy of a migrant bird, Barn Swallow, in Ireland, projected using temporally explicit temperature data and presence data using a generalised linear model (GLM). Barn swallow data extracted from 2018 presence records of eBird (2017) dataset (Sullivan et al., 2009), temperature data, monthly max and min values, extracted from Worldclim 2.0 database (Fick & Hijmans, 2017).

Several recent and thorough reviews within SDM explore the role of biotic interactions in model parameterisation using both correlative and joint-SDM (e.g., Wisz et al., 2013; Dormann et al., 2018;

Peterson et al., 2020), and as such it is not our aim to duplicate efforts. Instead, we highlight challenges and frontiers of incorporating biotic interactions within SDM and identify where phenological research could learn from this burgeoning field. The inclusion of biotic parameters (representing interactions or co-existence) in SDMs generally leads to improvement of predictive power of the models (Atauchi et al., 2017; Palacio & Girini, 2018), however, the fact that a model integrates biotic parameters does not always increase model accuracy (e.g., Holloway, 2018). In some cases when the considered biotic interactors are highly correlated to abiotic parameters, for example climatic conditions that determine presence of a particular species, the inclusion of biotic factors in model parameterisation might result in multicollinearity or show no improvements of SDMs due to the overarching influence of abiotic conditions (Silva et al., 2014). Recently, Raath, Le Roux, Veldtman and Greve (2018) compared four methods of incorporating biotic factors, by using different representations of host-plant distributions in SDMs of two silk moth species in sub-Saharan Africa. They found that inclusion of moth-host plant interactions in SDM greatly affected the predictive ability of the models, yet there was inconsistency among biotic representation. The inclusion of temporally explicit quantified biotic factors in SDM is rare (although note Mezquida, Svenning, Summers & Benkman (2018) who recorded the spatial timings of seed fall for European Scots pine and included this as a covariate in an SDM projecting the European distribution of crossbills), meaning studies have to rely on proxies for interactions within SDM. Thus, relevance of interactions and how interactions are represented in model parameterisation can shape the resulting outputs. With biotic representation a key component of our conceptual framework (Fig. 3), this subsequently warrants further research to investigate whether such patterns exist across multiple interactors and trophic levels within phenology.

7.2 Quantifying Interactions from New Technology

The use of new technology (e.g., acoustic recorders and telemetry data) has also been shown to provide novel insights for quantifying intra- and inter-species interactions (Isbell & Binder, 2016). Telemetry data acquires precise spatial and temporal animal position and movement data

627 (Hebblewhite & Haydon, 2010), having been used to capture information on phenological interactions,
628 such as mating, boundary patrolling, and hunting (Long & Nelson 2013; Benhamou, Valeix, Chamaillé-
629 Jammes, Macdonald & Loveridge, 2014 ; Long, Nelson, Weeb & Gee, 2014). Despite this advancement
630 in technology, similar issues relating to the direct estimate of intra- and inter-species-specific
631 interactions persists. For example, Miller (2012; 2015) tested several commonly implemented indices
632 of dynamic interactions for brown hyenas in Botswana alongside a null model of movement. The
633 results suggested that the use of 'expected' values in their generation produced inconsistent results,
634 which led to both Type I and II errors in the model interpretation. The general consensus has been
635 that such indices perform well at identifying no interaction between individuals; however, the majority
636 of these models use proximity in space and time (i.e. co-existence) to infer interaction, meaning similar
637 issues of interaction contextualisation persist. However, indirect interactions through smell or sight
638 that impact movement behaviours (e.g., leading, following) are difficult to model due to the
639 hierarchical nature of the processes, and may be considered as 'no interaction' in established indices
640 due to the spatial and temporal asynchrony. New methods that consider the potential path area of
641 movement trajectories in temporally asynchronous space are being developed that allow for such
642 interactions to be quantified (Hoover, Miller & Long 2020).

643 Similarly, camera traps have also been used to capture information on phenology (e.g., Graham,
644 Riordan, Yuen, Estrin & Rundel, 2010; Tape & Gustine 2014; Alberton et al., 2017), allowing the
645 examination of community structures and interspecific interactions (Steinmetz, Seuaturien &
646 Chutipong, 2013; Jachowski, Katzner, Rodrigue & Ford, 2015; Buxton et al., 2016; Camargo-Sanabria
647 & Mendoza 2016). For example, Jachowski et al. (2015) used over 2.5 million images from over 180
648 camera traps to investigate interactions among raptor species (i.e. bald and golden eagle) in eastern
649 continental USA in relation to their migration phenology and subsequent interactions. By analysing
650 the presence of raptors in more than 2.5 million images, the authors found that bald and golden eagles
651 were positively associated with each other, with the presence of golden eagles 55% more likely if a
652 bald eagle was also sighted on the same day, suggesting a possible mutualistic interaction. The ability

of camera traps to capture observed interactions is a primary advantage to the technology. However, Koike et al. (2012) used camera traps to investigate herbivory by mammals of fruit produced by trees in Japan, and while the authors concluded that the animals visited the trees, the images did not necessarily confirm that the animals actually ate the fruit. Therefore, despite the potential of such technology, issues related to the quantification of the biotic interaction persist. Fig. 5 illustrates examples where camera traps, acoustic recorders, and telemetry data capture co-existence in space and time as well as direct interactions. New methods of quantifying these interactions, through image analysis, acoustic signals, and movement parameters will subsequently be needed to ascertain in what instances interactions can be recorded.

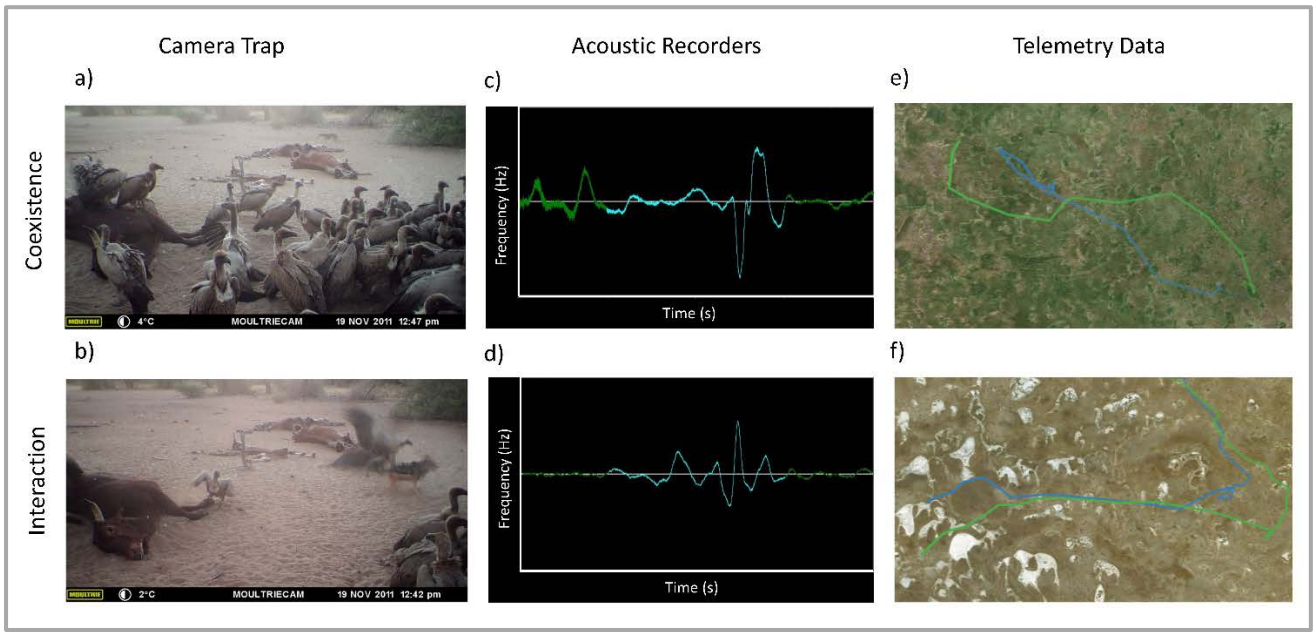

Figure 5. Illustration of co-existence between species versus biotic interactions using technology including camera traps, acoustic recorders, and telemetry data. Image captured from a camera traps in the Ghanzi region of Botswana, showing presence of black-back jackal and hooded vultures a) in the same location at same time, not interacting and b) an interaction (competition) between two individuals. Photo credit Thoralf Meyer. Audiograms from acoustic recorders (AudioMoth) (Hill et al., 2018) in Cork, Ireland, showing waveforms of recorded calls (green line), blue lines are the fragment of the calls analysed identifying vocalization, with SoundID (Boucher, 2014), c) illustrating co-existence, vocalizations of various individuals of two different *corvidae* species, jackdaw and rook, where no apparent interaction was taking place and d) illustrating interaction (competition) between jackdaws and rooks, with the audiogram reporting corresponding patterns for alarm and territorial calls. Global positioning system (GPS) of Burchill's zebra in Botswana, showing e) coexistence and f) interaction (herding) between individuals over a 24-hour period. Zebra data from Bartlam-Brooks et al. (2013a,b) via Movebank (2013), visualised in DYNAMO-Vis (Dodge, Xavier & Wong, 2018).

673 Remote sensing has also been widely used in phenology research, primarily to document phenological
674 events for vegetation, such as start-of-season or end-of-season (O'Connor, Dwyer, Cawkwell &
675 Eklundh, 2012; Barrett et al., 2014; Misra, Buras, Heurich, Asam & Menzel, 2018) or through the use
676 of active sensors (e.g., radar) to monitor animal migration events (e.g., Diehl, Larkin & Black 2003;
677 Schmaljohan, Liechti, Bächler, Steuri & Bruderer, 2008; Nilsson et al., 2018). These phenological
678 indicators (e.g., start-of-season, first-flight) are then used to identify spatial or temporal asynchronies
679 between interactor species or used as spatial representations of biotic factors in statistical models
680 (Morellato et al., 2016). UAV footage can be monitored to quantify interactions between individuals,
681 with Schofield, Katselidis, Lilley, Reina and Hays (2017) investigating whether departure of male turtles
682 from breeding sites was driven by changes in the receptiveness of females or the probability of
683 successful mating attempts, quantifying this through the sex ratio of all individuals within the footage.
684 Subsequently, drones offer a (relatively) non-invasive method to monitor phenological events of
685 inaccessible species. Remote sensing has also been used successfully to monitor species invasions
686 (Rocchini et al., 2015) through the reflectance properties of vegetation to classify different species to
687 identify competition among native and non-native species (e.g., Carter et al., 2009) and to identify
688 pest or disease emergence (e.g., He, Chen, Potter & Meentemeyer, 2019), with interactions inferred
689 through these indirect observations. Challenges associated with novel methods of classifying
690 hyperspectral images to delineate among plant species or identify pest-induced plant stress have been
691 identified as perhaps being more important than challenges associated with the resolution of such
692 data (Rocchini et al., 2015), which would allow for an improved species-level monitoring of
693 phenological events. However, the question of how to directly record inter-species interactions
694 through remote sensing remains, in part due to the relatively coarse-level data obtained from remote
695 sensing compared to the scale many biotic interactions occur at, suggesting a need for integration of
696 multiple technologies to address such challenges.

697 Integration of multiple technologies will provide new forms data on interactions among individuals,
698 populations, and species, which will then require novel methodologies for analysis. For example, Isbell

and Bidner (2016) used a combination of camera traps, acoustic recorders, and telemetry data to investigate the interactions between vervet monkeys and leopards in Kenya. Alarm calls recorded through the acoustic recorders revealed that these occurred most frequently at dusk and dawn, while camera traps revealed that leopards approached vervets most frequently at night when alarm-calls were initiated less. Telemetry data then identified the direction of movement of leopards associated with corresponding alarm calls from the acoustic devices, finding that when alarm calls were present, leopards moved quickly away up to 200m. Such a novel study identifies a successful framework for overcoming the individual limitations of each of the technologies, allowing interactions to be confirmed. However, the authors did not generate any quantification of these interactions, providing a qualitative description of the measurements. Such approaches could be extended to explore interactions directly related to phenological events, such as breeding success for prey species. Reviews are emerging that explore the utility of combining acoustic recorders with camera traps (Buxton et al., 2016), and technological advancements are combining GPS collars with remote cameras to provide context to interaction (Hebblewhite & Haydon 2010). The International Cooperation for Animal Research Using Space (ICARUS) has also recently launched, aiming to utilise satellite and tracking technology to observe the movement of small animals, providing a global approach to animal movement, which will undoubtedly provide new insights informing phenology and biotic interactions. Marion et al. (2020) provide an up-to-date review of methods for studying human-wildlife interactions using camera traps and telemetry data, with recommendations potentially applicable to studying biotic interactions in phenology research. It is evident that such interdisciplinary approaches are needed in this emerging research field.

8. Concluding remarks

Our review summarizes the current state of the art for methods employed for the evaluation of phenology and biotic interactions. We document a noticeable imbalance among both topics; phenology and biotic interactions, despite the important role biotic interactions have in phenological

processes, and vice versa. While studies investigating biotic interactions in phenology are relatively scarce, several studies across disparate disciplines have undertaken research, and can be broadly grouped into four main categories: 1) spatial and temporal asynchronies, 2) biotic factors as covariates, 3) simulation studies, and 4) interaction indices. Spatial and temporal mismatch studies have typically used historical datasets to infer changes in biotic interactions that are not measured from co-occurrence records (Gordo & Sanz, 2005) or SDM projected into future space and time to investigate changes in distributions among interactor species (Yun et al., 2020). Biotic factors as covariates studies have focused on trophic or obligated interactions since any change in one interactor is expected to have impact on the other (Post & Forchamer, 2007). However, experimental studies testing both abiotic and biotic factors are still rare (Alexander et al., 2015). Simulation studies of phenological events and biotic interactions are rare and have mainly been developed to test for changes in phenological events under different climatic scenarios (Bateman et al., 2016) or to evaluate changes in ecological networks by removing biotic components (Schleuning et al., 2016). Novel approaches developing interaction indices can help to develop new methodologies to document phenological events at broad regional scales (Buxton et al., 2016) as well as providing new insights for the monitoring of biotic interactions. Finally, we introduce a new framework that apportions biotic interactions into two interconnected factions where research is aimed towards 1) conceptualising biotic interactions within phenology and 2) modelling biotic interactions within phenology. Such a framework should provide researchers and practitioners with a basis to investigate interactions and co-existence successfully and robustly within the wider field of phenology.

8. Author contributions

RTC and PH conceptualised this review. RTC conducted the systematic portion of the review and wrote the first draft of the paper. PH provided inputs and helped in the editing process of the manuscript. Both authors were involved in the revision process.

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10. Data Availability

All data used to create figures are currently in open repositories. Data for figure 4 was extracted from ebird (2017) and WorldClim 2.0 database (Fick & Hijmans, 2017). Zebra data for figure 5 was from Bartlam-Brooks et al. (2013a, b) via Movebank (2013).

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